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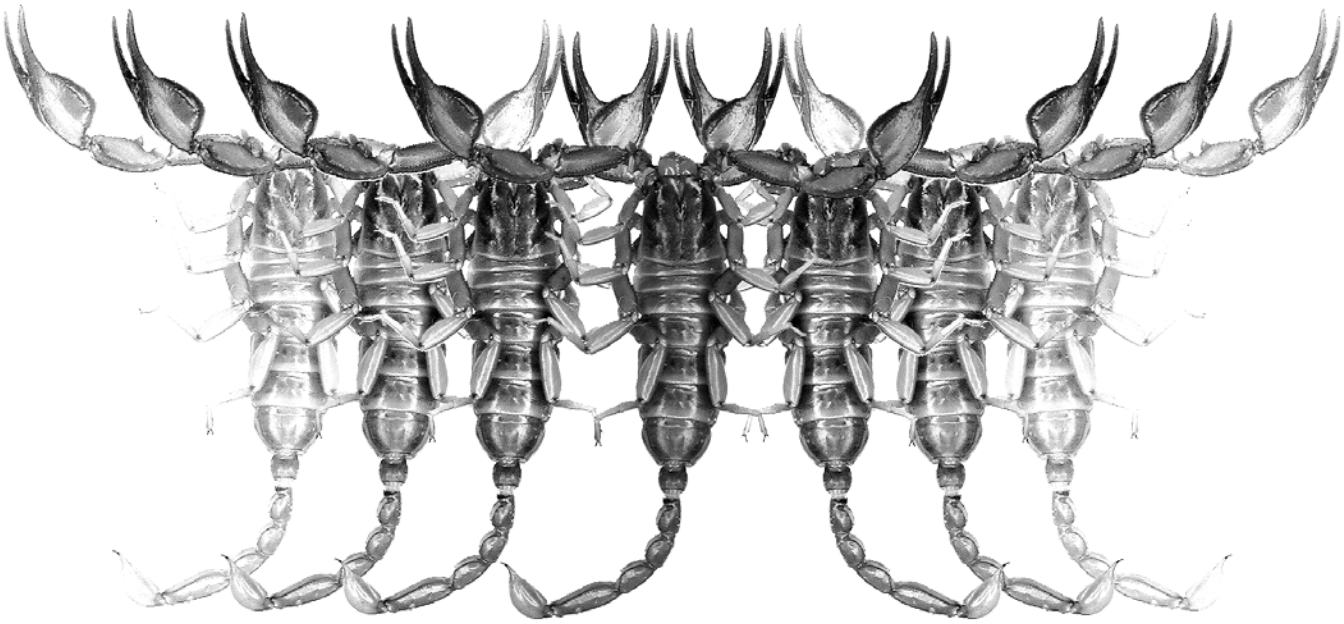

Prey Capture Behavior in the East African Scorpions *Parabuthus leiosoma* (Ehrenberg, 1828) and *P. pallidus* Pocock, 1895 (Scorpiones: Buthidae)

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Prey capture behavior in the East African scorpions *Parabuthus leiosoma* (Ehrenberg, 1828) and *P. pallidus* Pocock, 1895 (Scorpiones: Buthidae)

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Summary

Prey capture behavior in *Parabuthus leiosoma* (Ehrenberg, 1828) and *P. pallidus* Pocock, 1895 was studied in the laboratory. The behavioral components involved in prey capture were identified and an ethogram is presented. The occurrence of the different prey capture components are analyzed and discussed.

Introduction

Scorpions are efficient predators that accept a wide variety of prey (Polis & McCormick, 1986; McCormick & Polis, 1990). Most species are nocturnal and hunt prey by the use of a sit and wait strategy, where prey is either located in the opening of the scorpion's burrow/hiding place or just outside it. Only a few species are reported to actively hunt prey away from their hiding place (McCormick & Polis, 1990).

The ecological aspects of prey capture and foraging in scorpions have been thoroughly investigated by the late Gary Polis and associates (see Polis, 1990 and McCormick & Polis, 1990 for a review). Also, the sensory-physiological aspects of prey capture are well documented by the studies by Philip Brownell, Douglas Gaffin and others (see reviews in Brownell, 2001 and Gaffin & Brownell, 2001). The behavioral aspects of prey capture have been less documented and most studies have been anecdotal in nature, or just have included brief descriptions of prey capture for different species (see McCormick & Polis, 1990 for a review). One exception is Bub & Bowerman's (1979) study on prey capture in *Hadrurus arizonensis* Ewing, 1928 (Iuridae). In this study, the different behavioral components involved in the prey capture were identified and discussed. Cushing & Matherne (1980) and Casper (1985) have also provided some quantitative data for some of the behavioral components of the prey capture sequence.

The purpose of this paper is to present a quantitative analysis of the behavior components involved in prey capture in *Parabuthus leiosoma* (Ehrenberg, 1828) and *Parabuthus pallidus* Pocock, 1895 from East Africa.

Methods

Natural history

Parabuthus leiosoma (Fig. 1) and *P. pallidus* (Fig. 2) are found in several countries in East Africa (Probst, 1973). Adults of the former species are of medium size for scorpions and have yellow to yellowish-red body, except for part of the metasoma and telson which are dark red/brown. They have small, slender pedipalps and a thick, powerful metasoma. *Parabuthus pallidus* is superficially similar in coloration and morphology but is slightly smaller and lacks the darkened distal part of the metasoma. Except for Rein (1993), there are no previous reports on the biology of these species. *Parabuthus leiosoma* was previously named *P. liosoma*, but according to Fet & Lowe (2000) the correct name should be *P. leiosoma*.

Materials

Individuals of *Parabuthus leiosoma* and *P. pallidus* were collected in the vicinity of Isiolo, Kenya in May and June of 1988. The animals were found in the same semi-arid area under stones along roadsides, but no more than one scorpion was ever found beneath a single stone. The substrate consisted of compacted sand with sparse grass and bushes. The scorpions were transported to Norway where 11 individuals of *P. leiosoma* and 12 individuals of *P. pallidus* were kept for observation. The

specimens were of unknown age and ranged in length (pro- and mesosoma) from 18 to 32 mm (mean, 25.1 mm, *P. leiosoma*) and 13 to 31 mm (mean, 21.3 mm, *P. pallidus*). Specimens were kept individually in terraria (32 x 20 cm), with a substrate of sand and some stones. The temperature was maintained at 24 to 30° C, and the daylight period was 10 to 14 hours. Water was provided weekly by misting. Animals were not fed except when tested. Only animals active on the surface in the dark period were selected for experiments. This appeared to be a useful indication of hunger, since they usually responded rapidly when prey were offered.

For testing, the scorpions were transferred to an observation terrarium (25 x 25 cm) with sand as substrate. To prevent disturbance bias, they were given one hour for acclimatization before prey was introduced. Data on all activities were collected by direct observations under low intensity red light that is apparently not visible to scorpions (Machan, 1968). All observations were made during the fall 1988, and spring 1989.

Experiment

Prey capture was observed after presentation of three different types of prey that differed in size and morphology. These were small (10-18 mm) and large (24-32 mm) larvae of *Tenebrio molitor* Linnaeus and a centipede, *Lithobius forficatus* (Linnaeus) (26-35 mm). Insect larvae and centipedes were seen in the scorpions' habitat in Kenya, and thus are probably natural prey for the two *Parabuthus* species. After the acclimatization period, a live prey item was introduced to the test scorpion and, if accepted, observations were made until ingestion started. The scorpions were allowed to complete ingestion before they were returned to their terrarium. If a scorpion did not accept the prey, the test was discontinued, and the animal was returned to its terrarium.

Results/Discussion

The behavioral components involved in prey capture in *Parabuthus leisoma* and *P. pallidus* were identified and an ethogram was constructed (fig. 3). The same behavioral components were seen in both species, so only one common ethogram is presented. The following behavioral components were identified. Terminology and definitions are based on the terms of Bub & Bowerman (1979); if different, their corresponding terms are listed in parentheses:

Active (Motile + Alert stance): Locomotion within the terrarium prior to contact with prey, or the scorpion is standing still with the trunk raised above the substrate, pedipalps outstretched in front of the animal, and the movable fingers of the hand and pectines in contact with the substrate. Metsasoma is curved above the scorpion's back (in a more outstretched and offensive position than in the passive position).

Passive (Retracted): Body in contact with the substrate, appendages drawn in. Metasoma is either in a passive position above the body, or curved to the side of the body.

Orientation: Detection of prey and movement of the scorpion resulting in the anterior aspect of the body being directed towards the prey.

Grasp attempt: An attempt to seize and hold prey with one or both pedipalps.

Grasp failure: Prey escapes the scorpion after grasp attempt, regardless whether there has been any contact or not.

Grasp success: Scorpion obtains a firm hold of the prey with one or both pedipalps.

Sting attempt (Not used by Bub & Bowerman, but included in "sting"): The scorpion moves the aculeus against the prey by a forward sweep of the metasoma, either over the mesosoma or on the side of the trunk until contact with prey is established.

Figure 1: *Parabuthus leiosoma* (Ehrenberg, 1828) in the active position

Figure 2: *Parabuthus pallidus* Pocock, 1895 eating a prey.

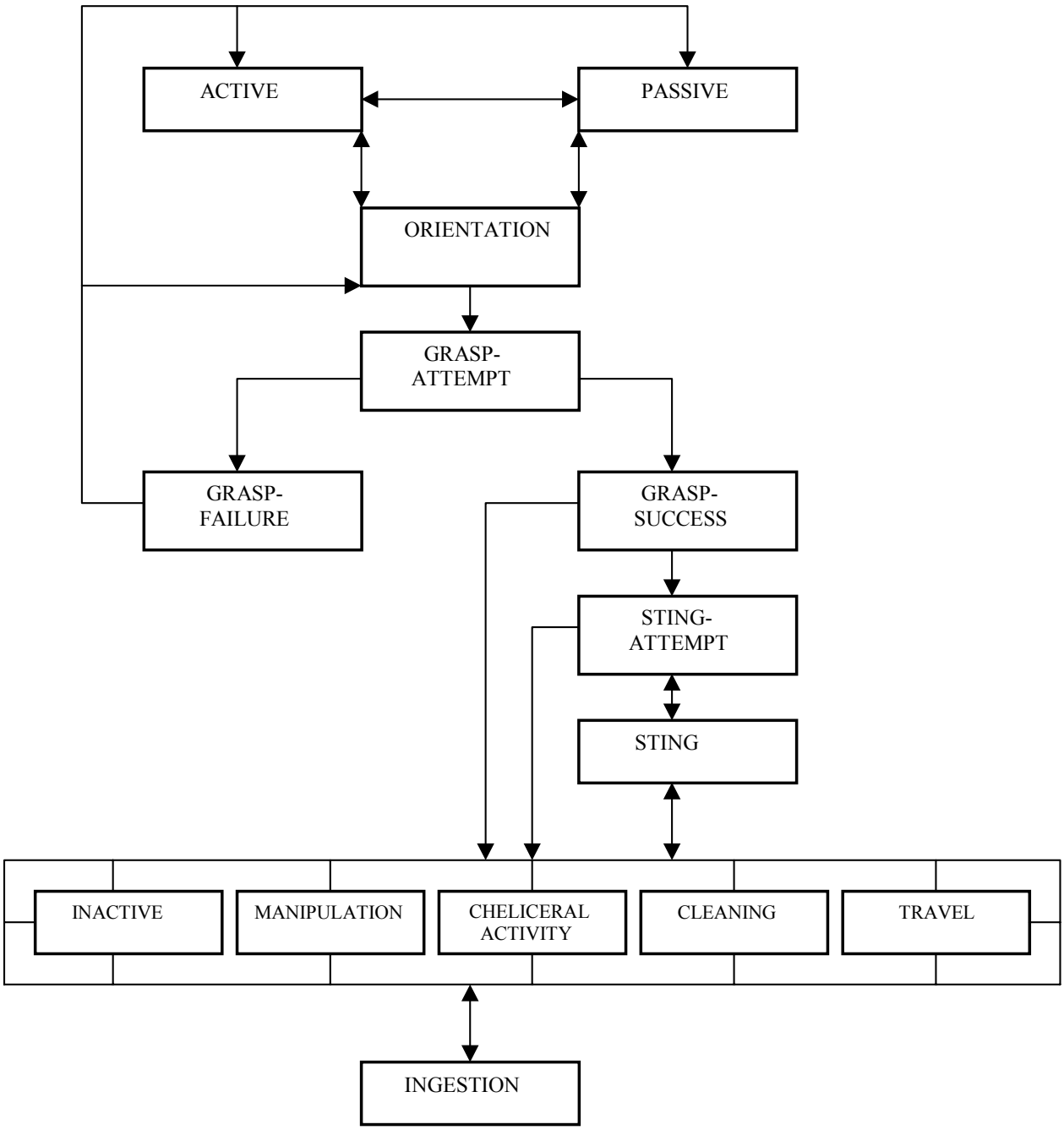

Figure 3: Ethogram showing the behavioral components in prey capture in *Parabuthus leiosoma* and *P. pallidus*. The behavioral components are defined in the text. Arrows indicate the direction of the prey capture sequence. The framing of the behavioral components inactive, manipulation, cheliceral activity, cleaning and travel refers to any of these behaviors observed either prior to, or after any of the others.

When contact is obtained, penetration of skin with the stinger is attempted immediately. If the skin of the prey is hard or smooth, the aculeus is repeatedly moved back and forth against the prey's body with "nodding" movements until a soft spot is detected. If this attempt fails during a short time, the metasoma is moved back from the prey or back into normal position. If metasoma is moved against the prey again with subsequent penetration attempts, this is classified as a new sting attempt.

Sting: Successful sting attempt: Penetration of prey with the aculeus and presumed injection of venom.

Inactive: Following a successful grasp attempt and sting, the scorpion holds the subdued prey with one or both pedipalps and no visually detectable activities are seen. This behavior could last for a few minutes to several hours.

Manipulation: The chelicerae, pedipalps and/or first pair of legs are used to change the original position of the prey relative to the chelicerae.

Cheliceral activities: Protraction of one chelicera and retraction of the second, alternating with retraction of the first and protraction of the second. The chelicerae are opened during protraction and closed during retraction.

Cleaning (Sand thrust): One or both pedipalps and/or aculeus are pushed into the substrate and frequently moved back and forth a few times. In some cases this behavior is ended with the involved pedipalp or aculeus being brushed against the trunk or legs.

Travel: Movement throughout the cage, holding the prey in the pedipalps and/or chelicerae. Alternatively, the scorpion leaves the subdued prey, moves away from it, and then returns to continue foraging. Both types of travel were seen in the same prey capture sequence in some of the trials.

Ingestion: Intake of the pre-digested fluid prey, as indicated by cyclical movements of coxae of the first legs.

Prey capture sequence

When observations started after the acclimatization period, the scorpions were in the active position in 41.4 % (*P. leiosoma*, n = 58) and 46.3 % (*P. pallidus*, n = 80) of the trials. In the rest of the trials, the scorpions had chosen the passive position. Prey were accepted in both positions, but the scorpions seemed more alert in the active position. In nature, the passive position is probably mostly seen when the scorpions are in an inactive state in their burrows and hiding places. The passive position seen in these trials might be caused by the experimental situation or that the scorpions were not motivated for prey capture due to insufficient hunger level.

When prey was detected, the anterior part of the body was positioned facing the prey. The scorpion then moved against the prey and attempted to grasp it with one or both pedipalps. Not all orientations against prey resulted in grasp attempt. Three types of detection and capture of prey were observed:

A. Prey was detected and grasped immediately (time < 0.5 sec.) after direct contact with a part of the scorpion's body.
B. The presence of the prey was first ignored by the scorpion, in spite of physical contacts between the two, and prey was captured later in the trial.
C. Prey was detected from a distance (> 1 cm). The scorpion oriented toward the prey, walked in the direction of the prey and grasped it as soon as it was within reach of the pedipalps.

Table 1 presents the occurrence of the different detection types. There were very few observable detections of prey at a distance (Type C), and in most trials either type A or B was observed for the different prey types. There were also no obvious differences between the two species in the way they detected prey.

Scorpions detect their prey with the help of substrate vibrations and some species can detect prey up to a distance of 50 cm (Brownell, 1977; Brownell & Farley, 1979). During most of these trials, there were no observable signs of prey detection from a distance. Prior-contact detection of prey may not be the case in all species, and also not on all types of substrate (surface waves are more easily detectable on soft sand than on harder substrates). It is therefore possible that the observed post-contact detection of prey is normal for many scorpions (i.e. that prey has to touch the scorpion, or come very close to touching, before prey capture is elicited).

The slow response to the presence of the prey might also be due the experimental situation. Many individuals froze in the inactive position during transportation to the observation terrarium, and it is possible that one hour of acclimatization was too short for the scorpions to recover. It is possible that the scorpions need stronger stimuli to initiate prey capture when they are in this position/state or remain in a "test setting".

Another explanation for the delay in response might be the test specimens' hunger state. Stahnke (1966) reported that hungry scorpions had quicker responses and were more aggressive than satiated individuals. The latter category was docile and often did not react to nearby insects. It is possible that scorpions with insufficient hunger levels will need stronger stimuli from prey to react, while hungry scorpions will react much quicker to the presence of prey. Unfortunately, it was not possible to correlate the scorpions hunger level (i.e. time since last feeding) with response type in this study.

Grasp failure rarely happened when scorpions had detected prey and attempted capture. When this happened, the scorpions either attempted to locate and grasp the prey again, or just adopted the active or passive po-

Prey type		A	B	C	n
Small larvae	*P. leiosoma*	4	13	1	18
	P. pallidus	9	16	4	29
Large larvae	*P. leiosoma*	8	5	4	17
	P. pallidus	8	12	3	23
Centipede	*P. leiosoma*	13	8	2	23
	P. pallidus	14	11	3	28

Table 1: Types of detection of prey in *Parabuthus leiosoma* and *P. pallidus*. A: Prey was detected and grasped immediately (time < 0.5 sec.) after direct contact with a part of the scorpion's body, B: The presence of the prey was first ignored by the scorpion, in spite of physical contacts between the two, and prey was captured later in the trial, C: Prey was detected at a distance (> 1 cm). The scorpion oriented towards the prey, walked in the direction of the prey and grasped it as soon as it was within reach of the pedipalps. n = number of trials.

sition and paid no more attention to the prey.

Following successful grasp attempt, the stinger was used in some trials. A restrictive sting use was observed. Decreased use of the stinger occurred with decreasing size/resistance of the prey. Also, prey was not stung immediately after being seized, but only after resisting capture. The scorpions did not sting non-resistant prey. Prey that were not stung were devoured alive. A detailed analysis and discussion of the sting use in these two *Parabuthus* species were presented in Rein (1993), and will not be discussed further here.

The scorpions were inactive after successful grasp attempts in 3.5 % (*Parabuthus leiosoma*, n = 58) and 2.5 % (*P. pallidus*, n = 80) of the trials. This position is identical to the passive position, except that the scorpion holds the subdued prey in one or both pedipalps. The inactive position was always observed immediately after the scorpion had gained control over the prey, and the scorpions stayed inactive from 30 seconds to several hours.

Cushing & Matherne (1980) observed that *Parurocto-nus boreus* (Girard, 1854) (Vaejovidae) stayed inactive for 10-30 minutes after rendering the prey harmless, but gave no explanation for this behavior. The low incidence of this behavior in two *Parabuthus* indicates that this is not a normal behavior, but rather a result of the experimental situation. An alternative explanation is that the scorpion stays inactive after prey capture to let the venom work before starting ingestion. This explanation is not supported by the fact that most prey were subdued within 30 seconds after sting use in this study and within one minute in *Paruroctonus boreus*.

Table 2 shows the occurrence of travel with prey after successful prey capture. In these cases, the scorpion carried the subdued prey in one or both pedipalps, or in the chelicerae away from the place where the prey was initially grasped. This behavior was more common in *Parabuthus pallidus* than in *P. leiosoma*, regardless of prey type. A second type of travel was observed in *P. pallidus* where the scorpion released the subdued prey, walked around in the cage for a while, and then returned back to prey and continued the prey capture sequence.

Several species are reported to ingest prey at the site of capture, while others carry prey away, usually to sheltered places under vegetation or back to their burrows (Bub & Bowerman, 1979; Le Berre, 1979; McCormick & Polis, 1990). The data from this study suggest that *P. leiosoma* belongs to the first category, while *P. pallidus* moves prey away after capture. This was supported by the fact that *P. pallidus* usually carried prey back to their burrows when fed in their individual terrarium. A possible advantage of moving prey into a more secure location is that the scorpion is less vulnerable to predation.

Travel without prey after successful capture is not previously described. An explanation for this behavior is that the scorpion needs to recover after encounters with hard struggling prey. Centipedes have venomous jaws, and it was observed in a few cases that the scorpions released the centipedes after being bitten. An alternative explanation is that this is not a natural behavior and a result of the scorpions being disturbed in the laboratory. In all cases, the scorpions returned directly to the prey without any problem and seemed to know the position where the prey was dropped.

Cleaning behavior was observed in both species (Table 3), but was more common in *Parabuthus pallidus*. Generally, this behavior was more often seen with the large prey types. Cleaning behavior was first described by Bub & Bowerman (1979), who named it sand thrust. They assumed that it had a role in cleaning the pedipalps, but did not discuss this any further. In addition to the pedipalp sand thrust, a similar behavior involving the metasoma was observed in this study. After a successful sting, many individuals straightened the metasoma posteriorly and rubbed the aculeus back and forth in the

Prey type		*P. leiosoma*	*P. pallidus*
Small larvae	With prey	2 (18)	10 (29)
	Without prey	0 (18)	0 (29)
Large larvae	With prey	0 (17)	15 (23)
	Without prey	0 (17)	2 (23)
Centipede	With prey	4 (23)	18 (28)
	Without prey	0 (23)	5 (28)

Table 2: The occurrence of travel with or without subdued prey after prey captures in *Parabuthus leiosoma* and *P. pallidus*. The numbers in parentheses represent number of trials.

Prey type	*P. leiosoma*	*P. pallidus*
Small larvae	0 (18)	11 (29)
Large larvae	6 (17)	16 (23)
Centipedes	7 (23)	16 (28)

Table 3: The occurrence of cleaning behavior during prey capture in *Parabuthus leiosoma* and *P. pallidus*. The numbers in parentheses represent number of trials.

sand. This behavior has not been described in previous studies.

Scorpions have numerous hairs (setae) on their body, especially on the pedipalps. Many of these hairs are innervated and play an important role in the sensory system of scorpions (Brownell, 1977, 1979, 2001). These hairs will move when exposed to external vibrations (e.g. substrate vibrations from moving prey), and it is possible that these movements are impaired if hairs are exposed to body fluid from injured prey. This might reduce sense capabilities or irritate the scorpion. Small drops of body fluid were observed on the stinger and pedipalps during prey capture in many of the trials. These exposures were always followed by sand thrust, involving either the pedipalps or the metasoma. It is therefore reasonable to conclude that the sand thrust is a sort of cleaning behavior with the purpose of removing irritating substances from the pedipalps and/or metasoma. The cleaning behavior was seen more often with the large prey types, which can be due to the stronger resistance in these making the prey capture "messier".

Manipulation of large larvae was done by both species in more than half of the trials. Small larvae were manipulated in only one third of the trials by both species, while the manipulation frequency varied between the species in the trials with the centipedes. *Parabuthus leiosoma* manipulated centipedes four times, while this happened 12 times in *P. pallidus*.

Several authors have argued that manipulation of prey is necessary for the scorpion to orient prey so that it can be ingested from the head end. Alexander (1972) reported a 91% head-first ingestion in *Opistophthalmus latimanus* C. L. Koch, 1841 (Scorpionidae), and Bub & Bowerman (1979) had similar observations in *Hadrurus arizonensis*, with a 89% head- first ingestion. In the latter case, head-first ingestion usually involved manipulation of prey before consumption.

In this study, the starting point for ingestion varied between the types of prey and between the species (Table 4). No clear preference for prey orientation was observed. In both species, head-first ingestion was as common as "other" when the scorpions captured small

A.

Prey	Head	Rear	Other
Small larvae M = 5 (n = 18)	9	1	8
Large larvae M = 10 (n = 17)	8	3	6
Centipede M = 4 (n = 23)	4	12	7

B.

Prey	Head	Rear	Other
Small larvae M = 7 (n = 29)	13	4	12
Large larvae M = 14 (n = 23)	6	4	13
Centipede M = 12 (n = 28)	9	9	10

Table 4: Manipulation and orientation of prey after capture. A. *Parabuthus leiosoma*, B. *P. pallidus*. M = number of trials in which scorpion manipulated prey before start of ingestion. n = total number of trials. "Other" denotes all parts of the prey excluding the anterior and the posterior part of the prey. See text for further explanation.

larvae. In these cases, "other" meant that the chelicerae of the scorpions were able to grasp the legs of the larvae, or its body.

Alexander (1972) did not discuss any advantages underlying a head-first consumption behavior, but Bub & Bowerman (1979) suggested that this behavior might assist in subduing the prey by immediately damaging the brain. They also suggested that this behavior could reduce the risk of injury by orthopteran prey having large and powerful hindlegs or prey with posterior chemical defenses.

The results of the present study indicate that prey orientation is dependent upon successful cheliceral grasp. Manipulation of prey was observed when the chelicerae had problems of grasping the prey. Large *Tenebrio* larvae are very hard and smooth, consequently cheliceral grasp was difficult on the smooth integument. This might explain the high incident of manipulation in this prey type. The large larvae were manipulated until the chelicerae got hold, which was usually accomplished in the prey's anterior or posterior. Centipedes have powerful jaws, but the scorpions did not avoid the head end. Instead, the scorpions started ingestion where it was easy for the chelicerae to securely grasp. This was quite easy throughout the centipede body due to the numerous legs and, especially in *Parabuthus pallidus*, the results support this conclusion. It must be added that the centipedes used in this study were not large enough to endanger the scorpions, their bites caused only irritation.

Bub & Bowerman's (1979) suggestion that head-first ingestion in scorpions would help subdue the prey quickly because of the destruction of the prey's brain is less likely. Firstly, the venom of the scorpions usually renders prey helpless within seconds. Secondly, due to the construction of arthropod nervous system with several major ganglia along the body, the destruction of the brain will not necessary stop a prey from fighting back due to neural activities in the remaining ganglia.

The prey types used in this study were quite similar in body shape (long, thin and flexible), and this may have biased the results. A follow-up study using a wider variation of prey types would strengthen the conclusions drawn in these trials.

Ingestion started as soon as the chelicerae maintained a proper hold of a part of the body of the prey. The observations were discontinued thereafter.

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